# SOCIAL LIFE AMONG THE INSECTS[1]

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## LECTURE III—BEES SOLITARY AND SOCIAL

TO those who are not entomologists the word "bee" naturally signifies the honey-bee, because of all insects it has had the most delightful, if not the longest and most intimate association with our species. Of course, the key to the understanding of this association is man's natural appetite or craving for sweets and the fact that till very recently honey was the only accessible substance containing sugar in a concentrated form. It is not surprising, therefore, that man's interest in the honey-bee goes back to prehistoric times. He was probably for thousands of years, like the bears, a systematic robber of wild bees till, possibly during the neolithic age, he became an apiarist by enticing the bees to live near his dwelling in sections of hollow logs, empty baskets or earthen vessels. Savage tribes keep bees to-day and within their geographic range we know of no people that has not kept them. They figure on the Egyptian monuments as far back as 3500 B. C., and we even know the price of strained honey under some of the Pharaohs. It was very cheap—only about five cents a quart.

The keeping of the honey-bee could not fail to excite the wonder and admiration of primitive peoples. It was at once recognized as a privileged creature, for it lived in societies like those of man, but more harmonious. Its sustained flight, its powerful sting, its intimacy with the flowers and avoidance of all unwholesome things, the attachment of the workers to the queen—regarded throughout antiquity as a king—its singular swarming habits and its astonishing industry in collecting and storing honey and skill in making wax, two unique substances of great value to man, but of mysterious origin, made it a divine being, a prime favorite of the gods, that had somehow survived from the golden age or had voluntarily escaped from the garden of Eden with poor fallen man for the purpose of sweetening his bitter lot. No wonder that the honey-bee came in the course of time to symbolize all the virtues—the perfect monarch and the perfect subject, together constituting the perfect state through the exercise of courage, self-sacrifice,

[1] Lowell Lectures.

affection, industry, thrift, contentment, purity, chastity—every virtue, in fact, except hospitality, and, of course, among ancient peoples bent on maintaining their tribal or national integrity, the fact that bees will not tolerate the society of those from another hive was interpreted as a virtue.

With the passing centuries the bee became the center of innumerable myths and superstitions. It was supposed to have played a rôle in the lives of all the more important Egyptian, Greek and Roman divinities. Among the Latins it even had a divinity of its own, the goddess Mellonia. Medieval Christians seem to have been quite as eager to show their appreciation of the insect. While the housefly had to be satisfied with the patronage of Beelzebub and the ant was given so obscure a patron saint as St. Saturninus, the honey-bee enjoyed the special favor of the Virgin or was even made the "*ancilla domini,*" the maid-servant of the Lord. Those who represented the divinity on earth, of course, added the honey-bee to their insignia. It appears on the crown of the Pharaohs as the symbol of Lower Egypt, on the arms of popes and on the imperial robes of the Napoleons. Among the ancients the behavior of bees was supposed to be prophetic and the insect thus naturally became associated with Apollo, the Delphic priestess, the Muses and their protegées, the poets and orators. Honey and wax were early believed to have medicinal and magical properties and were, of course, used for sacrificial purposes. Their ritual value is apparent also in the Christian cult, for honey was formerly given to babies during baptism and the tapers of our churches are supposed to be made of pure bees' wax ("*nulla lumina nisi cerea adhibeantur*").

Among the many myths that have grown up around the honey-bee, that of the "bugonia" may be considered more fully, because it shows how entomology may throw light on questions that have puzzled and distracted the learned for centuries. For nearly three thousand years people believed that the decomposing carcass of an ox or bull can produce a swarm of bees by spontaneous generation. The myth evidently started in Egypt and appears in a distorted form among the Hebrews, among whom, however, it is a dead lion in which Samson finds the honey-comb. Among the Greeks and Romans it becomes more elaborate, and Virgil, in the fourth book of the Georgics, and many other authors give precise directions for the killing and treatment of the ox if the experiment is to be successful. The medieval writers repeat what they read in the classics or invent more fantastic accounts. It was not till the eighteenth century that Réaumur showed that what had been regarded as bees issuing from the decomposed ox carcass must

have been large two-winged flies of the species now known as *Eristalis tenax,* which breed in great numbers in carrion and filth and look very much like worker bees. The history of this myth of the oxen-born bees has been more adequately discussed by a distinguished dipterist, Baron Osten Sacken. He remarks that "the principal factor underlying the whole intellectual phenomenon we are inquiring into is the well-known influence which prevails in all human matters, and this factor is *routine.*" "Thinking is difficult, and acting according to reason is irksome," said Goethe. People see and believe in what they see, and the belief easily becomes a tradition. It may be asked: If those people had that belief, why did they not try to verify it by experiment, the more so as an economical interest seemed to be connected with it? The answer is that they probably did try the experiment, and did obtain *something* that looked like a bee; but that there was a second part of the experiment, which, if they ever tried it, never succeeded, and that was, to make that bee-like something produce honey. If they did not care much about this failure, and did not prosecute the experiment any further, it is probably because, in most cases, they found that it was much easier to procure bees in the ordinary way. That such was really the kind of reasoning which prevailed in those times clearly results from the collation of the passages of ancient authors about the "*Bugonia.*"

It would seem that the strange vitality of the bugonia myth during so many centuries must have been due to some keen emotional factor or religious conviction deeper than the mere inertia of routine thinking to which Osten Sacken refers. Let us work backwards from the golden bees embroidered on the state robes of Napoleon I and supposed to symbolize his official descent from Charlemagne, who is said to have worn them on his coat of arms. It is probable that the fleurs-de-lys, which also figure on his arms and those of the later French kings are really conventionalized bees and not lilies, spear-heads or palm trees with horn or amulets attached, as some archeologists have asserted, and that Charlemagne derived his bees from one of the first kings of the Salian Franks, the father of Clovis, Childeric I, who died A. D. 481. In 1653 the tomb of this monarch was opened at Tournay, in Flanders, and found to contain a number of objects which indicated that he had been initiated into the cult of Mithra, that soldiers' religion which had been so widely diffused by the Romans over Gaul, Britain and Germany during the first centuries of our era and had come so near to supplanting Christianity. Among the objects taken from Childeric's tomb were a golden bull's head and some 300 golden bees, set with precious stones and provided with clasps which held

them to the king's mantle. Now the numerous Mithraic monuments that have been unearthed in many parts of the Roman empire show as their central figure Mithra slaying a bull surrounded by several symbolic animals, one of which is the bee. It is known also that honey was used in the initiation rites of Mithra, who was an oriental sun-god like the Hebrew Samson, the Phoenician Melkart and the Greek Hercules. From the blood of the slain bull, a symbol of the inert earth fertilized by the sun's rays, the animal world was supposed to have arisen by spontaneous generation. The bee would seem, therefore, to be one of the symbols of this renewal of life and to recall the epiphanies of many other sun and vegetation gods among the Greeks and Asiatic peoples, such as Adonis, Attis and Dionysus, or Bacchus, who as Dionysus Briseus, the "squeezer of honey-comb" was by some regarded as the god of apiculture. But the bugonia myth can be traced still further back to the Apis cult of the Egyptians. The bull Apis was believed to be an incarnation of the sun-god Osiris and to represent the renewal of life. His son Horus is another sun-god, and it is interesting to note that one of his symbols is the fleur-de-lys, which signifies resurrection. That this is the true meaning of the bugonia myth is indicated also by the magical directions given by Virgil and others for slaying the ox and caring for his carcass. The animal must be carefully chosen and in the spring, when the sun is in the sign of the bull, clubbed to death or suffocated by having the apertures of his body stuffed with rags—obvious precautions to prevent the ox's vitality from escaping so that it may be conserved for the generation of the swarm of bees. The ancients seem to have had an inkling of the parthenogenesis of the honey-bee, since many of them state that, unlike other animals, it never mates. This belief, too, served to connect the bee with the various sun and vegetation gods, all of whom, including the bull Apis, were born of virgins. Thus it will be seen that the bee became the symbol of the ever-recurring resurrection, or renewal of life in general and hence probably also of the second birth of the initiate into such cults as those of Mithra. Unfortunately there were among the ancients no entomologists to point out to the religious enthusiasts that they had mistaken a common carrion fly for the honey-bee and had therefore chosen a wrong symbol.

I have dwelt on this myth because it is such a good example of the bad observation and worse conjecture that have clouded our knowledge of the honey-bee. Even such pioneer observers as Swammerdam, Réaumur and François Huber in the seventeenth and eighteenth centuries and Dzierzon, Leuckart, von Siebold and von Buttel Reepen in more recent times have had difficulty in

clearing a path through the jungle of superstitions and speculations that have grown up around the insect during the past five thousand years. And to-day many of our scientific treatises contain vestiges of these unbridled fancies. Another obstacle to a clear understanding of the honey-bee is the very abundance of the literature. There must have been libraries devoted to it among the ancients, for even Carthage had her celebrated apiarists. Some notion of the present conditions may be gleaned from Dr. E. F. Phillips' statement that the Bureau of Entomology at Washington has a working bibliography of 20,000 titles on the honey-bee. This does not, of course, include a great number of bellettristic works like Virgil's Georgics, Maeterlinck's "Vie des Abeilles" and Evrard's "Mystère des Abeilles."

Greatest of all the sources of a misunderstanding of the honey-bee is the fact that although it is a very highly specialized and aberrant insect, it has been regarded as a paragon in the light of which the social organizations of all other insects are to be interpreted. Its evolutionary interpretation has therefore encountered the same obstacles as that of man, for the honey-bee bears much the same relation to other bees that man does to the other mammals; and just as man's obstinate anthropocentrism has retarded his understanding of his own history and nature, so the apicentrism of the observers of the honey-bee has tended to distort our knowledge, not only of other social insects but of the honey-bee itself. It is necessary, therefore, to relegate the insect to its proper place at the end of a long series of developments. I shall return to it at the end of the lecture.

As classified by the entomologists, the bees comprise about 10,000 described species and occur in all parts of the world. In Europe alone there are some 2,000 species and our North American forms, when thoroughly known, will probably be found to be even more numerous. Less than 500, or 5 per cent., of the 10,000 species are social and belong to only five genera—Trigona, Melipona, Bombus, Psythirus and Apis—the remainder being solitary forms of many genera, several of which are very large and widely distributed. For more than a century talented entomologists have studied the bees intensively but have been unable to work out any generally acceptable grouping of the various genera. Whether these insects are to be regarded as a superfamily (Apoidea), comprising several families, or as a single family (Apidæ), comprising a number of subfamilies, seems to depend on the individual investigator's more radical or more conservative frame of mind.

The bees, taken as a whole, are properly regarded merely as a group of wasps, which have become strictly vegetarian and feed

exclusively on the pollen and nectar of flowers. They are, in a word, merely flower-wasps—"Blumenwespen," as they are called by some German entomologists. A recent authority, Friese, believes that they are descended directly from at least two different ancestral groups of Sphecoid solitary wasps, one of which includes genera like Passaloecus and leads up to Prosopis and other primitive bees, while the other comprises Tachytes-like forms and leads up to the higher bees. It should be noted that a third ancestral group of Vespoids, allied to the Eumenid wasps, evidently gave rise to the Masarinæ, which are also flower-wasps and in their habits closely resemble the solitary bees.

Their very long and intimate association with the flowers has left its stamp on all the organs and habits of the bees, and botanists believe that a great many flowers have been modified in structure, arrangement, color and perfume in adaptation to the bees and for the purposes of insuring cross-pollination. Limitations of time prevent me from dwelling on the vast and fascinating subject of these relationships, though they belong to that order of interorganismal cooperation which I have called coenobiotic. Nor can I stop to dwell on our great debt to the bees for the pollination of our fruit trees and other economic plants. Something must be said, however, concerning the anthophilous adaptations of the insects themselves. It is evident that only insects with well-developed wings, with large, finely facetted eyes and well-developed antennæ, furnished with extremely delicate tactile and olfactory sense-organs, could have acquired such intimate relations to the flowers. And since the bees not only collect but transport the pollen and nectar we find some very interesting structures developed for these particular functions. Two pairs of mouth parts, the maxillæ and especially the tongue, are peculiarly modified for lapping or sucking up the nectar. In the more primitive bees that visit flowers with exposed nectaries these parts are short and much like those of the wasps, whereas in more specialized species that visit flowers with nectaries concealed in long tubes the tongue is greatly elongated. In some tropical bees the organ may be even longer than the body (Fig. 34). In order to store the nectar while it is being transported to the nest, the crop, or anterior portion of the alimentary tract, is large, bag-like and distensible and its walls are furnished with muscles which enable the bee to regurgitate its content. This is known as honey, because the nectar, during its sojourn in the crop, is mixed with a minute quantity of a ferment, or enzyme, presumably derived from the salivary glands, and undergoes a chemical change, its sucrose, or cane sugar being converted into invert sugars (levulose and dextrose).

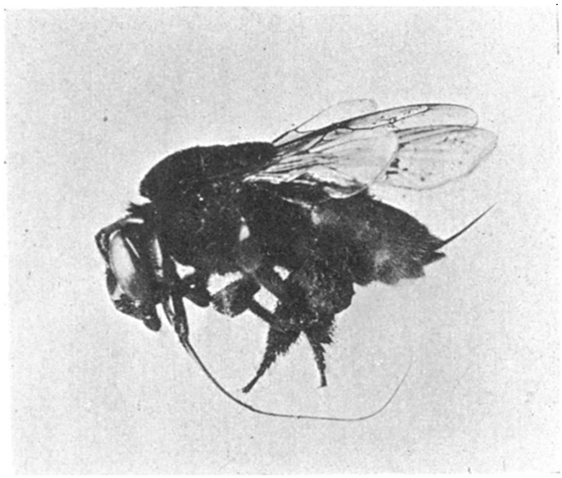

FIG. 34
A long-tongued Neotropical bee (*Eulaema mussitans*). About twice natural size. Original.

Even more striking are the adaptations for collecting and carrying the pollen. The whole surface of the bee's body is covered with dense, erect hairs, which, unlike those of other insects, are branched, plumose, or feather-like and easily hold the pollen grains till the bee can sweep them together by combing itself with its legs (Fig. 35). Many bees thus bring the pollen together into masses moistened with a little honey and attach them to the outer surfaces of the tibiæ and metatarsi of the hind legs (Figs. 37 and 38). These parts are peculiarly broadened and provided with long hairs to form a special pollen-basket, or corbicula (Fig. 36). In other

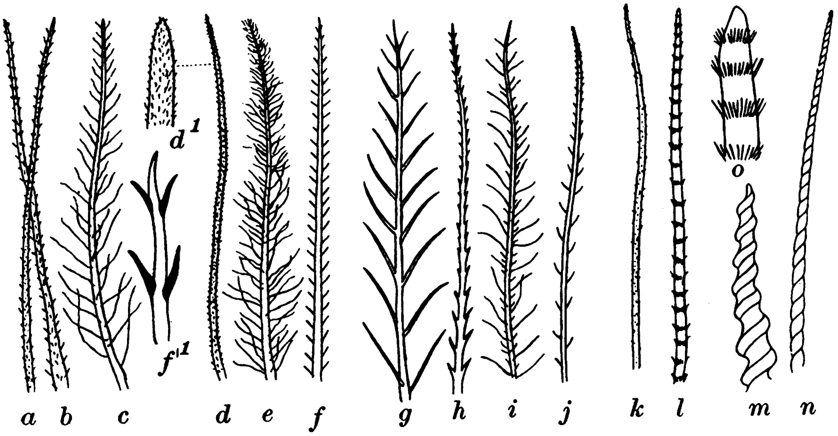


FIG. 35
Hairs of various bees. *a-f,* of bumble-bees; g-j, of *Melissodes* sp.; *k-n,* of *Megachile* sp. After John B. Smith.

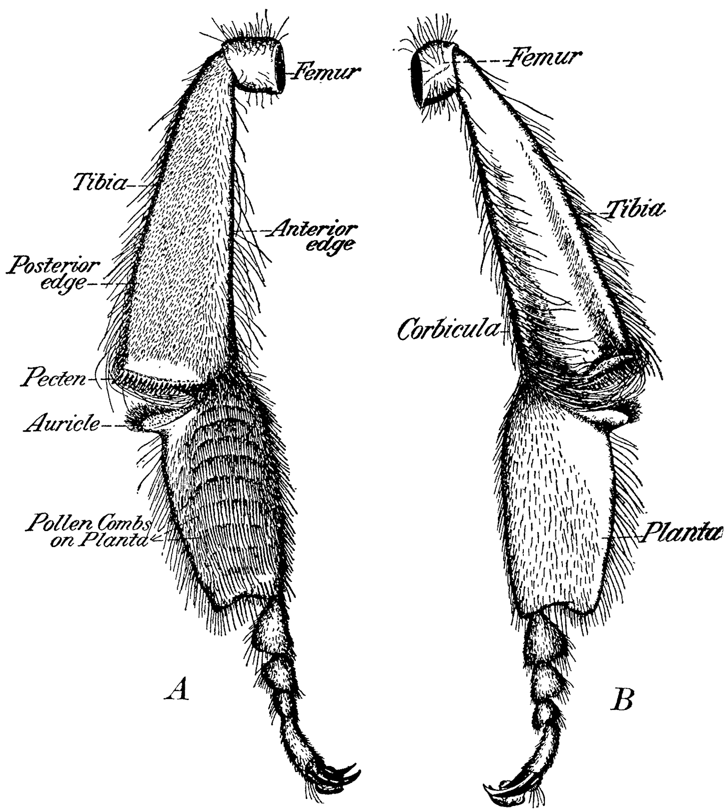


FIG. 36
*A*. Inner surface of the left hind leg of a worker honey-bee; *B*. Outer surface of the same. After D. B. Casteel.

bees the pollen is swept to the ventral surface of the abdomen, where there are special hairs for holding it in a compact mass. The bees of the former group are therefore called "podilegous," the latter "gastrilegous." That these various structures, *i. e.*, the general body investment of plumose hairs and the modifications of the hind legs or venter are special adaptations for pollen collection and transportation is proved by certain interesting exceptions. Thus the small bees of the very primitive genus Prosopis look very much like diminutive wasps; they have naked bodies and appendages and their hind legs are not modified. But these bees swallow the pollen as well as the honey and carry both in their crops. Then there is a long series of genera of parasitic bees which lay their eggs in the nests of the industrious species and on this account do not need any collecting or transporting apparatus. Such bees are more or less naked and their tibiæ have returned to the simple structure seen in the wasps. And, of course, since

male bees in general do not have to collect pollen we find that they, too, show considerable reduction in the hind legs as compared with the cospecific females.

There are great differences among the bees in the range of their attachment to the flowers. Some, like the honey-bee and the bumble-bees, visit all sorts of flowers and are therefore called polytropic, whereas others, the so-called oligotropic species, may confine their attentions to the flowers of a very few plants or even to those of a single species. The oligotropic are probably derived from polytropic bees which have found it advantageous to avoid competition with other species and to make their breeding season coincide with the blooming period of a single plant. A good example is one of our small black bees, *Halictoides novæ-angliæ* which at least in New England visits only the purple flowers of the pickerel weed, *Pontederia cordata.*

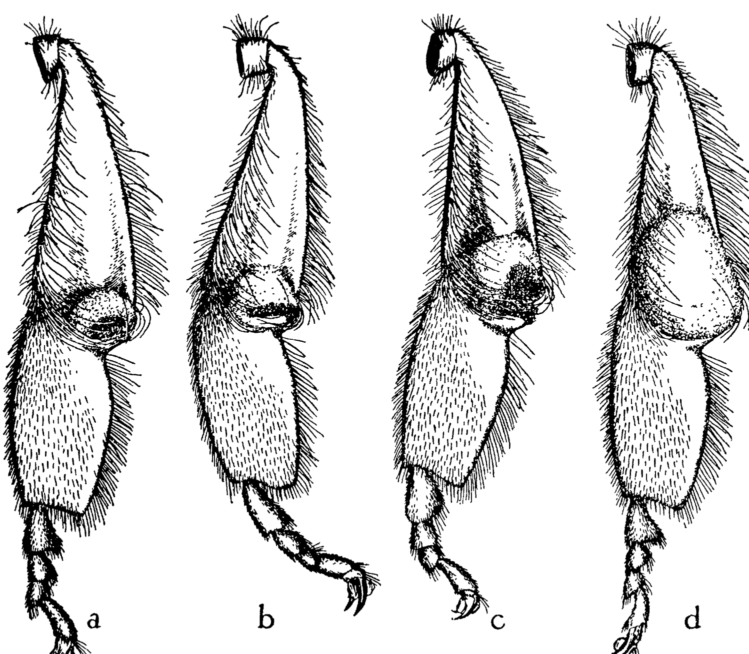


FIG. 37

Outer surfaces of left hind leg of worker bees in successive stages of pollen accumulation. *a,* from a bee just beginning to collect. The pollen mass lies at the entrance of the basket. The planta is extended, thus lowering the auricle. *b,* slightly later stage, showing increase in pollen. The planta is flexed, raising the auricle. The hairs extending outward and upward from the lateral edge of the auricle press upon the lower and outer surface of the small pollen mass, retaining and guiding it upward into the basket. *c* and *d,* slightly later stages in the successive processes by which additional pollen enters the basket. After D. B. Casteel.

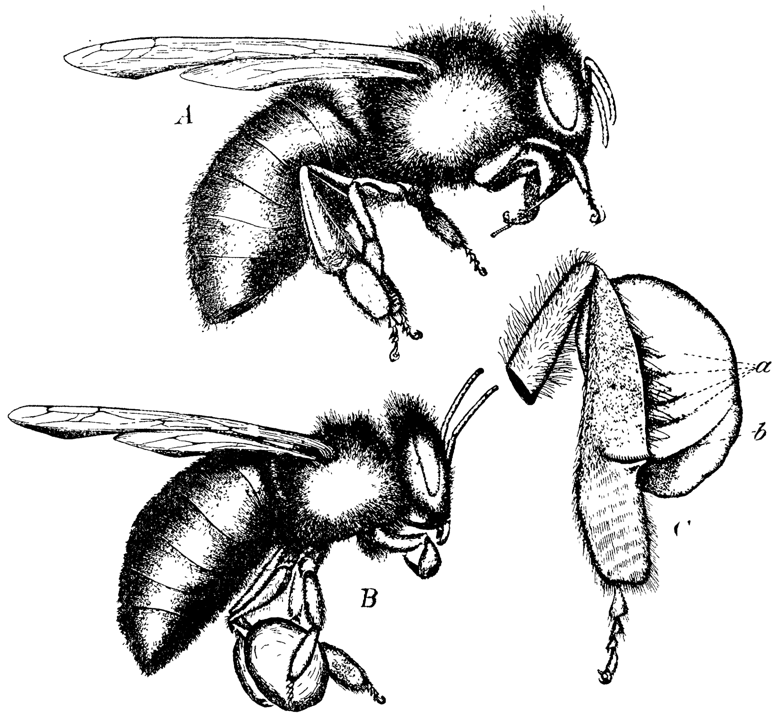


FIG. 38
Pollen manipulation of honey-bee. *A*. Flying bee, showing manner of manipulating the pollen with the fore and middle legs. The fore legs are removing the pollen from mouthparts and face; the right middle leg is transferring the pollen on its brush to the pollen combs of the left hind planta. A small amount of pollen has already been placed in the baskets. *B*. Flying bee showing portion of middle legs touching and patting down the pollen masses. *C*. Inner surface of hind leg bearing a complete load of pollen. *a*. Scratches in pollen mass caused by pressure of the long projecting hairs of the basket upon the pollen mass as it has been pushed up from below. *b*. groove in the pollen mass made by the strokes of the auricle as the mass projects outward and backward from the basket. After D. B. Casteel.

Turning now to the reproductive behavior which has led to the development of societies we find a most extraordinary parallelism between the group of bees as a whole and that of the wasps as described in my previous lecture. The progress from the solitary condition, shown in more than 95 per cent. of the species, to the conditions in the most highly socialized form, the honey-bee, is, so to speak, a repetition of the various wasp *motifs* set in a different key. Every one of the thousands of species of solitary bees has its own peculiarities of behavior, but the differences are usually so insignificant that the habits as a whole are very monotonous. With the exception of the parasitic bees, which have been secondarily evolved from non-parasitic forms, all the solitary bees make their

nests either in the ground or in the cavities of plants, in crevices of walls, etc., or construct earthen or resin cells (Fig. 39). Some species line their nest cavities with pieces of the leaves or petals of plants, with plant-hairs or particles of wood, or with films of secretion which resemble celluloid or gold-beater's skin. Most of these materials, as will be noticed, are derived from plants. The nest usually consists of several cylindrical or elliptical cells arranged in a linear series or more rarely in a compact cluster, and as soon as a cell has been completed, it is provisioned with a ball or loaf-shaped mass of pollen soaked with honey and called "bee-bread," an egg is laid on its surface and the cell is closed. We have here again the typical mass provisioning of the solitary wasps, very similar to that of the Eumeninæ, except that vegetable instead of animal substances are provided for the young. Nevertheless, the pollen and honey are ideal foods, since the former is rich in

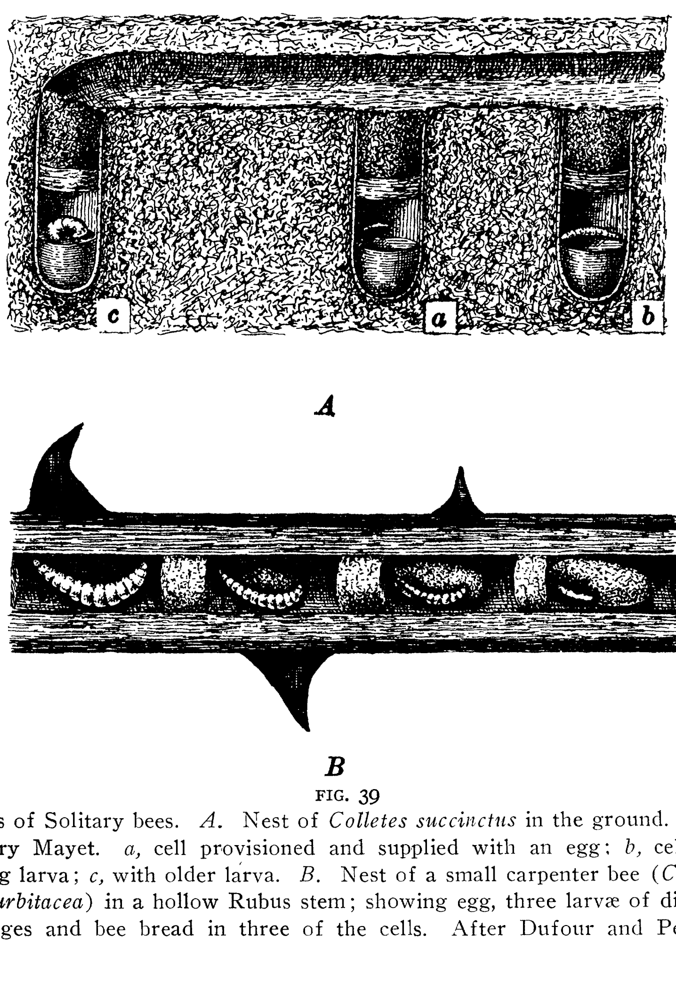


FIG. 39

Nests of Solitary bees. *A.* Nest of *Colletes succinctus* in the ground. After Valery Mayet. *a,* cell provisioned and supplied with an egg; *b,* cell with young larva; *c,* with older larva. *B.* Nest of a small carpenter bee (*Ceratina curcurbitacea*) in a hollow Rubus stem; showing egg, three larvæ of different stages and bee bread in three of the cells. After Dufour and Perris.

proteids and oils and the latter in sugar and water, and both contain sufficient amounts of various salts for the growth of the larvæ. As in the case of the solitary wasps the mother bee dies before her progeny emerge.

Just as among the solitary wasps, we often find female solitary bees nesting in close association with one another, and in some species (*Halictus longulus, Panurgus, Euglossa, Osmia vulpecula* and *parietina, Eucera longicornia*) the females, though occupying separate nests, nevertheless build a common entrance tunnel. Still there is nothing in these arrangements to indicate that they could lead to the formation of true societies. There are, however, a few cases which might be regarded as sub-social, since the mother bee survives the development of her progeny and shows more interest in their welfare than is implied by the mere mass provisioning of the cells. Two such cases are represented by the European *Halictus quadricinctus,* observed by Verhoeff, and *H. sexcinctus,* observed by Verhoeff, von Buttel Reepen and Friese. The female of the former bee digs a long vertical tunnel in the ground and at its lower end a chamber in which she constructs a number of earthen cells, arranged in the form of a rude comb. These cells of which there may be as many as 16 to 20, are successively provisioned and closed, but the mother is long-lived, guards the nest and may even survive till the young emerge. Hence there is here an actual though apparently very brief contact of the mother with her adult offspring.

Certain peculiarities in the life-history of Halictus may be conceived to tend still further towards social development. According to our present unsatisfactory knowledge of these bees, at least some of the species have two annual generations. The spring generation consists of fecundated females that have over-wintered from the previous fall. These give rise to a summer generation consisting entirely of females. Their eggs develop parthenogenetically, but produce both males and females, forming the fall generation. The males soon die, but the fecundated females go into hibernation. As von Buttel Reepen suggests, a society might be readily established in a form like *H. quadricinctus* if the parthenogenetic generation of females were to remain with their mother and extend the parental nest. This would be essentially what we find in the lower social wasps like Polistes.

A still more interesting case has been found by Dr. Hans Brauns among the bees of the genus Allodape which belong to the gastrilegous division and are closely related to our small carpenter bees of the genus Ceratina, so abundant in hollow stems of the elder and sumach. Dr. Brauns made his observations in

South Africa, where he has been living for many years, and kindly sends me the following unpublished data for use in this lecture:

"The species of Allodape nest in the dry, hollow stems of plants, very rarely in galleries in the soil. In both cases they gnaw out cavities or occupy those already in existence. Plant stems with pithy contents, like those of Rubus, Liliaceæ, Aloe, Amaryllidaceæ, Asparagus, Acacia thorns, etc., are preferred. Three different groups of species may be distinguished according to the method employed in provisioning the young. These three groups may also prove to be useful as morphological sections of the genus, since the majority of Allodape species, especially the smaller ones, are very difficult to distinguish in the female sex. The males yield better characters, though there are few plastic characters in the genus. Most of the descriptions drawn from single captured specimens have little value. Fanatical describers, like some of your countrymen, merely make the work of the monographer more difficult or more unattractive or even well nigh impossible in a genus which is almost as monotonous as Halictus. The three different methods of provisioning which I have been able to establish are the following:

"(1) The most primitive species, observed only on a few occasions. The mother bee collects in the nest tube as much beebread in single loaves or packets as the larvæ will require up to the time of pupation, precisely as in other solitary bees, *e. g.*, as in Ceratina, the form most closely related to Allodape. The single food-packets are arranged one above the other in the hollow stem and each is provided with an egg. The larva holds itself to the food-packet by means of peculiar, long, segmental appendages, which I have called provisionally "pseudopodia," and consumes its single packet till it is time for pupation. The size of the packet corresponds to the size of the particular species, much as in Ceratina, and each packet nourishes only a single larva. The latter holds its appendages spread out like those of a spider and is closely attached to the packet like the larvæ of such solitary bees as Ceratina. So far there is no departure from the conditions in the solitary Apidæ. There is, however, one fundamental difference: Whereas Ceratina after provisioning and oviposition closes off each cell with a partition of gnawed plant materials and therefore makes a series of individual cells, Allodape *constructs absolutely no partitions*. The food-packets, each large enough for a *single larva* and each furnished with a *single egg,* though arranged in a linear series one behind the other in the nest tube, as in Ceratina, Osmia, etc., lie freely one on top of the other and are not separated by partitions of the materials above mentioned. The

lowermost packet is the oldest and is therefore usually found to bear a larva while each of the upper packets bears an egg. This difference, as you will admit, must be regarded as of fundamental importance. In these more primitive species the mother does not come into contact with the larva since the latter has been provided *once for all* with sufficient food to last it till it pupates, precisely as in the solitary bees and wasps. The pseudopodia can not therefore have the function of exudate organs but merely serve to attach the larva mechanically to the food-packet. This transition from isolated cells to a simple unseparated series of packets is, of course, very interesting and significant.

"(2) Rather common, small and medium-sized species. The mother bee glues a number of eggs, each by one pole and in a *half spiral row,* determined by the curvature of the tubular cavity, to the wall of the nest, usually near the middle, *i. e.*, a little above or a little below. One common species I have also seen occupying tubular cavities in the earth with a similar arrangement of the eggs. The hatching larvæ hold fast to the walls of the tube by means of their pseudopodia and *are all at the same level with their heads directed towards the entrance to the cavity.* From time to time the mother brings in a small lump of bee-bread and deposits it in the midst of the hungry heads. The larvæ therefore all eat *simultaneously of the same mass of bee-bread.* During their last moult the mature larvæ lose the pseudopodia and become pupæ, which come to lie one behind the other in the tubular nest cavity. In these species, therefore, the mother remains in continuous contact with the larvæ.

"(3) The majority of species, from those of small to those of the largest size. The mother bee lays her eggs singly and loosely on the bottom of the nest tube. In proportion to the size of the bee the eggs are very, one might say abnormally, large and seem to be laid at longer intervals. The mother bee feeds the individual larva, which *clasps the particle of bee-bread* with its two large pseudopodia so that it *has the food all to itself.* When a nest that has been occupied for some time by a mother bee, is examined, one or several larvæ, each with its own pellet of bee-bread, are found in the position I have described. Later the daughters help their mother in provisioning the larvæ. When the colony has become populous the cavity of the tube is found to be stuffed with larvæ and pupæ in all stages. The latest egg, however, almost always lies on the floor of the tube. And since the mother bees must always go to the bottom to feed the youngest larvæ, the contents of the tube are often intermingled, though the larger larvæ and the pupæ are mostly nearer the opening and therefore upper-

most. In these species, also, the larvæ lose the pseudopodia during the last moult."

Brauns's observation on Allodape are of great interest and importance because they reveal within the limits of a single genus a series of stages beginning with a mass-provisioning of the young, like that of the solitary bees and wasps, and ending with a stage of progressive provisioning. And not only has the latter led to an acquaintance of the mother with her offspring but in the third group of species described by Brauns to an affiliation of the offspring with the mother to form a cooperative family or society. It would seem that this condition must have had its inception, as Brauns suggests, in so simple a matter as the omission of the series of partitions which all other solitary bees construct between their provisioned cells. The final stage in which the individual larvæ are fed from day to day by the mother and her daughters with small pellets of food is not essentially different from what we shall find in the bumble-bees and certain ants.

Yet these rudimentary societies of certain species of Halictus and Allodape must not be regarded as the actual precursors or sources of the conditions which we observe in the three groups of social bees, namely, the Bombinæ, or bumble-bees, the Meliponinæ, or stingless bees, and the Apinæ, or honey-bees. Though these all belong to the podilegous division, no one has been able to point out their putative ancestors among existing solitary bees, and it is evident that we can neither derive them from one another nor from any single known extinct genus. Each possesses its own striking peculiarities and each is an independent branch from the ancestral stem now vaguely represented by the solitary bees. The bumble-bees are the most primitive, the honey-bees the most specialized, while the stingless bees exhibit a combination of primitive and specialized characters different from those of either of the other subfamilies. But just as all the social wasps differ from the solitary wasps in employing a peculiar nest material—paper—so the three groups of social bees differ from the solitary bees in using another peculiar nest material—wax. This material is, however, a true secretion, which arises in the form of small flakes from simple glands situated between the abdominal segments of the insects (Fig. 40). The three groups of social bees also agree in the structure of the hind tibia, the outer surface of which is not only broadened as in solitary forms but smooth and shining with recurved bristles along the edges (Fig 36). This is called the corbula and among solitary bees is known to occur only in Euglossa.

The bumble-bees represent a stage of societal development of the greatest interest to the evolutionist. Of these large insects

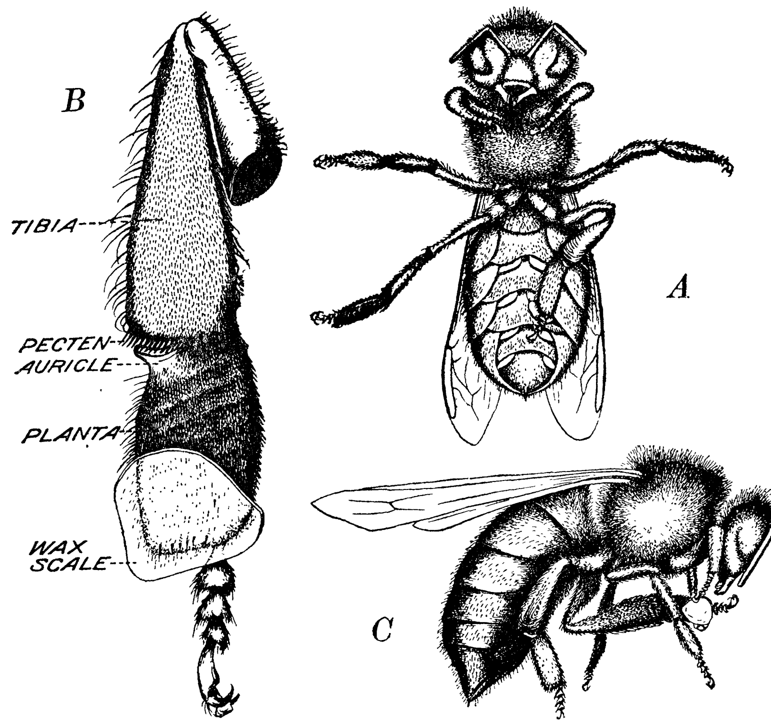


FIG. 40

A. Ventral view of worker honey-bee in the act of removing a wax-scale. B. Inner surface of left hind leg, showing the position of a wax-scale immediately after it has been removed from the wax pocket. The scale has been pierced by seven of the spines of the pollen combs of the first tarsal segment of the planta. C. Side view of a worker bee showing position of wax-scale just before it is grasped by the fore legs and mandibles. The scale is still adhering to the spines of the pollen combs. The bee is supported upon the two middle legs and a hind leg as in A. After D. B. Casteel.

about 200 species are known, mostly confined to Eurasia and North America. They prefer rather cool climates and several species occur in the arctic regions or at high elevations. Their habits have been carefully studied by several European entomologists, notably by Hoffer, Wagner, Lie-Petersen and Sladen, and are beginning to attract students in this country. We know very little about the species of Central and South America and the East Indies.

In temperate regions bumble-bee colonies are annual developments, like those of our northern species of Vespa and Polistes. The large fecundated female or queen overwinters precisely like the females of the solitary wasps and starts her colony in the spring. She chooses some small cavity in the ground or in a log, preferably an abandoned mouse-nest, and after lining it with pieces of grass or moss or rearranging the pieces already present, proceeds to the

important business of establishing her brood. The various stages in this behavior have been carefully observed by Sladen: "In the center of the floor of this cavity she forms a small lump of pollen-paste, consisting of pellets made of pollen moistened with honey that she has collected on the shanks (tibiæ) of her hind legs (Fig. 41*a*). These she moulds with her jaws into a compact mass, fas-

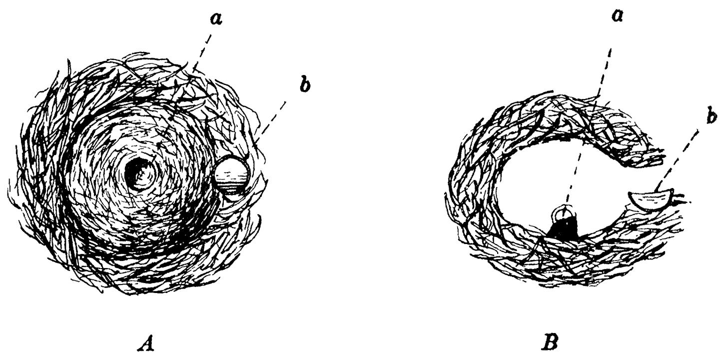


FIG. 41
Incipient nest of bumble-bee. *A*. Pollen and first eggs. *B*. Honey pot. After F. W. L. Sladen.

tening it to the floor. Upon the top of this lump she builds with her jaws a circular wall of wax, and in the little cell so formed she lays her first batch of eggs (Fig. 42*Ba*), sealing it over with wax by closing in the top of the wall with her jaws as soon as the eggs have been laid. The whole structure is about the size of a pea. . . . The queen now sits on her eggs day and night to keep them warm, only leaving them to collect food when necessary. In order to maintain animation and heat through the night and in bad weather when food can not be obtained, it is necessary for her to lay in a store of honey. She therefore sets to work to construct a large waxen pot to hold the honey (Fig. 41*b*, 43, 44). This pot is built in the entrance passage of the nest, just before it opens into the cavity containing the pollen and eggs, and is consequently detached from it. The completed honey pot is large and approximately globular, and is capable of holding nearly a thimbleful of honey."

Up to this point the behavior of the queen is much like that of the solitary bee which makes and closes her cell after providing it with provisions and an egg, but a significant change now supervenes. The eggs hatch after about four days and the further events are described by Sladen as follows: "The larvæ devour the pollen which forms their bed, and also fresh pollen which is added and plastered onto the lump by the queen. The queen also feeds them with a liquid mixture of honey and pollen, which she prepares by

swallowing some honey and then returning it to her mouth to be mixed with pollen, which she nibbles from the lump and chews in her mandibles, the mixture being swallowed and churned in the honey-sac. To feed the larvæ the queen makes a small hole with her mandibles in the skin of wax that covers them, and injects through her mouth a little of the mixture among the larvæ which devour it greedily. Her abdomen contracts suddenly as she injects the food, and as soon as she has given it she rapidly closes up the hole with the mandibles. While the larvæ remain small they are fed collectively, but when they grow large each one receives a separate injection."

Here we have a beautiful transition from mass to progressive provisioning. Sladen then describes the further development of the brood: "As the larvæ grow the queen adds wax to their covering, so that they remain hidden (Fig. 42 *BEb*). When they are about five days old the lump containing them, which has hitherto been expanding slowly, begins to enlarge rapidly, and swellings, indicating the position of each larva, begin to appear in it. Two days later, that is, on the eleventh day after the eggs were laid, the larvæ are full-grown, and each one then spins around itself an oval cocoon, which is thin and papery but tough (Fig. 42 *Cc*). The queen now clears away most of the brown wax covering, revealing the cocoons, which are pale yellow. These first cocoons number from seven to sixteen, according to the species and the prolificness of the queen. They are not piled one on another, but stand side by side, and they adhere to one another very closely,

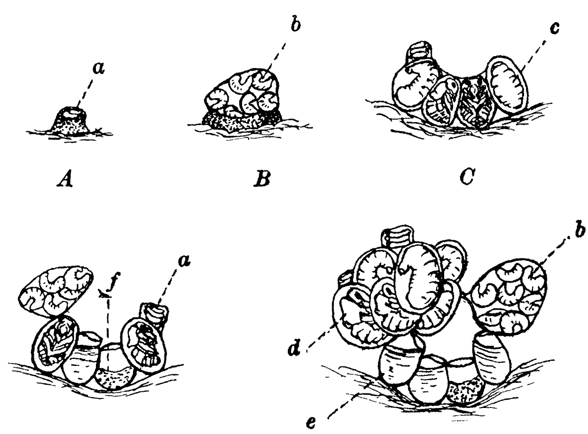


FIG. 42

*A* to *E*. Diagrams of successive stages in the development of the bumble-bee's brood. *a*, eggs; *b*, young larvæ; *c*, full grown larva; *d*, pupa; *e*, old cocoon used as a honey pot; *f*, old cocoon used as a pollen pot. After F. W. L. Sladen.

FIG. 43
Incipient nest of *Bombus terrestris,* showing honey-pot and mass of wax enclosing young brood and grooved for the accommodation of the body of the queen while incubating. After F. W. L. Sladen.

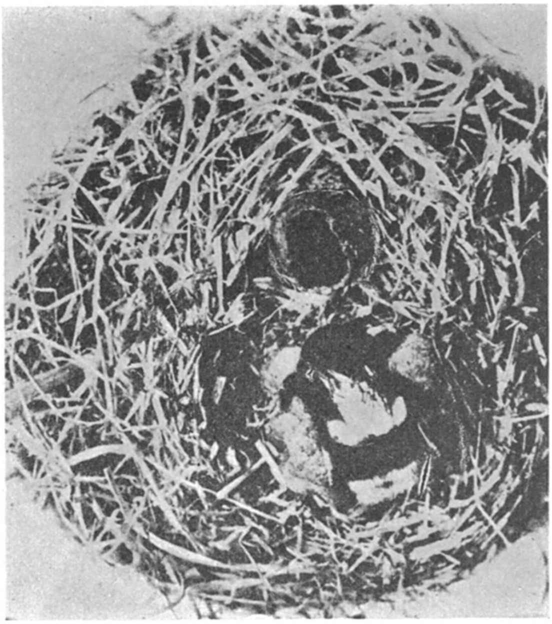

FIG. 44
Same as Fig. 43, showing the queen *Bombus terrestris* lying in the groove and incubating the young brood. After F. W. L. Sladen.

so that they seem welded into a compact mass. They do not, however, form a flat-topped cluster, but the cocoons at the sides are higher than those in the middle, so that a groove is formed; this groove is curved downwards at its ends (Fig. 43), and in it the queen sits, pressing her body close to the cocoons and stretching her abdomen to about double its usual length so that it will cover as many cocoons as possible; at the same time her outstretched legs clasp the raised cocoons at the sides (Fig. 44). In this attitude she now spends most of her time, sometimes remaining for half-an-hour or more almost motionless save for the rhythmic expansion and contraction of her enormously distended abdomen, for nothing is now needed but continual warmth to bring out her first brood of workers. In every nest that I have examined the direction of the groove is from the entrance or honey-pot to the back of the nest, never from side to side. By means of this arrangement the queen, sitting in her groove facing the honey-pot—this seems to be her favorite position, though sometimes she reverses it—is able to sip her honey without turning her body, and at the same time she is in an excellent position for guarding the entrance from intruders.''

The eggs laid by the queen during the early part of the summer are fertilized and therefore produce females, but the larvæ, owing to the peculiar way they are reared, secure unequal quantities of nutriment and therefore vary considerably in size, though

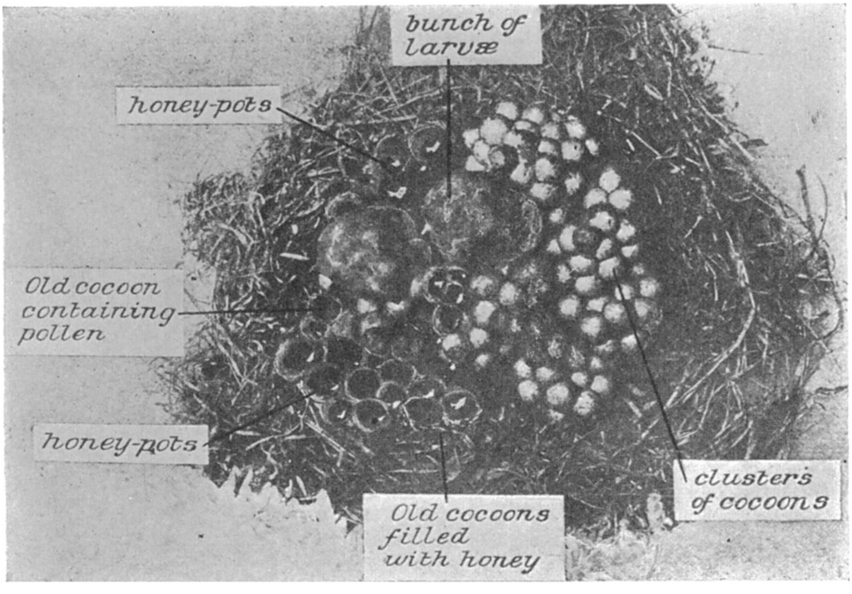


FIG. 45
Comb of *Bombus lapidarius,* showing clusters of worker cocoons, masses of enclosed larvæ, half-full honey-pots and pollen pot. After F. W. L. Sladen.

they are all smaller than their mother. Individuals scarcely larger than house-flies are sometimes produced, especially in very young colonies. All of these individuals have been called workers, although they have essentially the same structure as the queen. They are assisted in emerging from their cocoons by their mother or sisters and forthwith take up the work of collecting pollen and nectar and of enlarging the colony. The queen now remains in the nest and devotes herself to laying eggs, while the nest is protected, new cells are built and the additional broods of larvæ are fed by the workers. They also construct honey-pots and special receptacles for pollen or store these substances in cocoons from which workers have emerged (Fig. 45). Later eggs are also laid by the workers but being unfertilized develop into males. As the colony grows and becomes more prosperous, some of the larvæ derived from fertilized eggs laid by the queen are abundantly fed and develop into queens. Like the queens of the social wasps, these do not emerge from their cocoons till the late summer, and like the queen wasps, they disperse, after mating with the males, and alone of all the colony survive the winter to start new colonies the following spring. In South America, where, according to von Ihering, bumble-bee colonies are perennial, new nests are formed by swarming as among the social wasps of the same region. Bumble-bee colonies are, as a rule, not very populous, 500 individuals constituting an unusually large society. In many cases there are scarcely more than 100 to 200.

I have called attention to the fact that the workers are precisely like the queens, or fertile females, except that they have been more or less inadequately fed during their larval stages and are therefore smaller. They are the result of a high reproductive activity on the part of the queen under unfavorable trophic conditions that do not permit the offspring to attain their full stature. In certain species that live permanently under even more unfavorable conditions, like those in the arctic regions, the worker caste is completely or almost completely suppressed. During 20 years of residence in Tromsö, Norway, Sparre Schneider failed to find a single worker of *Bombus kirbyellus,* and those of *B. hyperboreus* were extremely rare. Probably the queens of these species are able to rear only a few offspring and these are all or nearly all males and queens, though, during the short arctic summer, at least in Finland and Lapland, the mother insects work late into the nights. But the worker caste may also disappear as a result of the opposite conditions, that is, an abundance of food. We found this to be the case with the workerless parasitic wasps, *Vespa arctica* and *austriaca.* In north temperate regions the genus Bombus has given rise to a

number of parasitic species, which have been included in a separate genus, Psithyrus. These bees are very much like Bombus, in the nests of which they live, but just as in the two species of Vespa and for the same reasons, their worker caste has been suppressed.

The foregoing account shows that the bumble-bees are very primitive and represent an interesting transition from the solitary to the social forms, since the queen while establishing her colony behaves at first like a solitary bee but later gradually passes over to a stage of progressive provisioning and affiliation of her off-spring and thus forms a true society. The cells are also essentially like those of solitary bees, except that they are made of wax, but even in the secretion of the wax the bumble-bees represent the primitive conditions, as compared with the stingless bees and honey-bees, since the substance is exuded between both the dorsal and ventral segments of the abdomen.